

THE RELATIONSHIP OF THE TERRESTRIAL JAWED
SANGUIVOROUS G. *MESOBDELLA* TO THE NEOTROPICAL
HIRUDINIFORM LEECHES (HIRUDINOIDEA)*

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Synopsis

The morphological relationships and morphology of the reproductive systems show that the affinity of *Mesobdella* is in the Neotropical hirudiniform leeches, and not the auriculate land-leeches of the *F. Haemadipsidae* of the Oriental and Australian Regions.

INTRODUCTION

After many studies, R. Blanchard (1917) assembled the sub-family Haemadipsinae for the terrestrial jawed sanguivorous leeches essentially in terms of habit and external morphology, with as criteria: a broad ocular arch of 5 pairs of eyes, 1 to 4 on contiguous annuli, 4 and 5 separated by two annuli; the nephropores lateral, the last concealed beneath auricles formed on each side by the fusion of the lateral ends of the incomplete uniannulate somites xxv to xxvii. The criteria separated the land-leeches from the aquatic and amphibious jawed sanguivores and the macrophagous leeches in the subfamily Hirudininae. The land-leeches continue in the same essential framework in the *F. Haemadipsidae* (Soos, 1967).

Ordered in this manner, the Haemadipsidae contains the land-leeches of the Oriental, Madagascan, Australian, and Polynesian zoogeographic divisions with, as a zoogeographic anomaly, the inclusion in the family of the Neotropical genera *Mesobdella* (Chile and Argentina) and *Nesophilaemon* (Juan Fernandez). This inclusion of the Neotropical genera has become increasingly suspect with the progressive demonstration by Ringuélet and by Caballero of the distinctive nature of the aquatic and amphibious jawed sanguivorous and macrophagous hirudiniform component in the leech fauna of the Neotropical Region.

Recently (Richardson, 1969a), it was shown that the reproductive systems as known in the Oriental, Madagascan and Australian auriculate land-leeches are distinctive in their morphology and morphological relationships: the median regions, hemimyomeric, the male an amyomeric micromorphic atrium, the female myomeric, formed on a posteriorly directed primary loop with a glandular sac developed as an expansion of the posterior face of the elbow of the loop, i.e., non-axial, asymmetric, and termed an oviducal glandular sac to distinguish it from the axial, symmetrical vagina formed along a limb of the primary loop in the hirudiniform leeches; in the land-leeches, the anterior region of the male paired duct forms a posteriorly directed primary loop in the median chamber, the epididymis on the recurrent limb, the sperm duct on the procurvent limb, these organs posterior to the atrium, not lateral to it and in the paramedian chamber as in the hirudiniforms.

With this, it was clear from Ringuélet (1955) that in *Nesophilaemon* the epididymis is lateral to the median regions and in the paramedian chamber; the female median region is myomeric, with a long common oviduct and an axial acaecate vagina extending over the posterior end of the recurrent limb and the full length of the procurvent limb. Accordingly, contrary to the

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indications from the presence of an "haemadipsine" ocular arch, a 4-annulate complete somite, and a duognathous condition, all as in the Australian g. *Philaemon*, the evidence from the reproductive systems show that *Nesophilaeon* cannot be retained in the Haemadipsidae.

At that time, I could not reach an opinion on the nature of the reproductive systems in *Mesobdella*. Having now had the privilege of studying specimens of *M. gemmata* in the collections of the Zoologisches Museum der Humboldt-Universität zu Berlin, I can give the characteristics of the g. *Mesobdella* as follows:

g. *Mesobdella* Blanchard, 1893. Fig. 1 A to E.

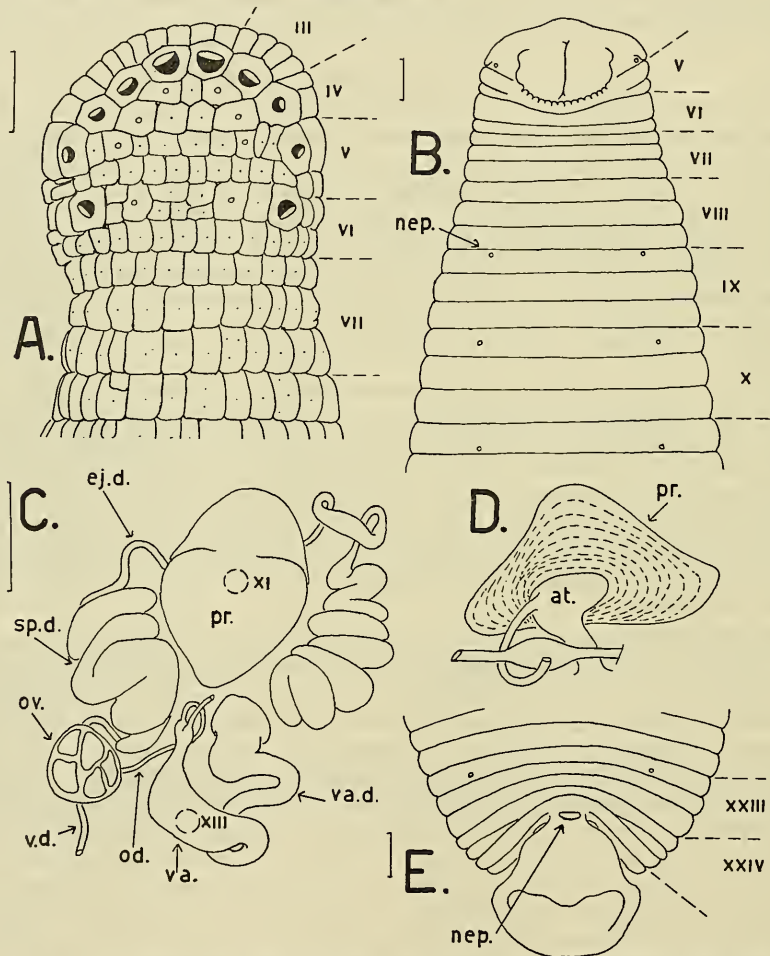


Fig. 1. *Mesobdella gemmata* (Em. Blanchard 1849). A. Dorsal aspect somites i to vii (Specimen, b); B. Ventral aspect, somites i to ix (Spec., a); C. Anterior region of male paired ducts, prostate, female median reproductive system (Spec., a); D. Longitudinal vertical section of male median region to show micromorphic atrium and laminate prostate (Spec., a); E. Ventral aspect of posterior portion of body and posterior sucker to show nephropores and annulation (Spec., c).

Somital ganglia and somites indicated by roman figures.

At., atrium; e.j.d., ejaculatory duct; nep., nephropore; od., oviduct; ov., ovary; pr., prostate; sp.d., sperm duct; v.d., vas deferens; va., vagina; va.d., vaginal duct.

All scales indicate 0.5 mm.

Monostichodont; trignathous; no salivary gland papillae; jaws, tall; teeth, minute, acute; somital sense organs, small, obscure; paramedian field, wide; ocular arch broad, eyes 1 to 4 on contiguous annuli, 4 and 5 separated by one annulus; vii to xxiii 3-annulate, complete (total 1 + 16); xxiv, incomplete 3-annulate; xxv and xxvi, incomplete 2-annulate; xxvii, incomplete uniannulate; no auricles; nephropores: 1st labial at iv/v, 2nd to 16th (as in the hirudiniforms) ventral on a_1 of ix to xxiii, 17th a single median ventral pore posterior in xxiv; dorsal salivary glands in compact right and left masses each with a large column of aggregated ducts; radial muscles sparse, in viii and some few in ix; pharynx, vi/vii to viii/ix, thin-walled, narrowly tubular, weakly muscular, smooth internally; crop, 2 short simple acaecate chambers in each of ix and x, single compartments each with a single pair of wide-based simple caeca in xi to xviii, paired simple elongate postcaeca on xix; no lambertian organs; genital pores, xi a_2/a_3 and xii/xiii (anterior in xiii a_1); testes, simple saccular; anterior region of paired male duct without a primary loop; sperm ducts linear in the paramedian chamber and lateral to the median regions; no sperm vesicles or ejaculatory bulbs; median regions, hemimyomeric; male atrium, amyomeric, micromorphic; female median region, myomeric, mesomorphic; oviducts long; atrium distinct; common oviduct lacking; axial acaecate vagina along the length of the recurrent limb of the primary loop, a long vaginal duct on the procurrent limb; prostate large, laminate; no albumin glands. Size, medium. Pattern, longitudinal stripes. Terrestrial. Sanguivorous. Neotropical Region.

Types species: *Hirudo gemmata* Em. Blanchard, 1849. Chile.

Other species: *M. uotohilica* Ringuelet, 1953. Argentina. (? *M. lineata* Sciacchitano, 1959. Transvaal).

The above is based on:

(a) Berlin Mus. Coll. Plate. No. 3934. Tub. 5. Chili (Corral) Leg Plate 1894. Det. Apathy. One specimen, total length 14.0 mm.

(b) Berlin Mus. Coll. Plate. No. 3934. Tub. D₁. *Mesobdella gemmata* (Em. Blanchard, 1849). Chili (Corral) Leg. Plate 1894. Det. Apathy. One specimen, total length 25.0 mm.

(c) Berlin Mus. No. 3935. *Mesobdella gemmata* (E. Bl.) Chili, Fritellar, Llanguihul. Plate 1895. Det. Apathy. One specimen, total length, 21.0 mm.

DISCUSSION

Mesobdella is "haemadipsine" in: general facies; ocular arch; wide dorsal median field; a clamp on the posterior sucker; labial position of the 1st nephropores; hemimyomeric median regions; absence of albumin glands.

Mesobdella is non-haemadipsine in: the small obscure somital sense organs detectable with confidence only on the ocular annuli; the small size of the posterior sucker; the 2-annulate condition of xxv and xxvi, the annuli fusing in each somite to a single annulus laterally and not forming auricles; the nephropores 2 to 16, ventral as in the hirudiniform leech; the median ventral common nephropore of the 17th pair of nephridia; the tall jaws; thin-walled narrow pharynx; sparse extrinsic musculature; acaecate double compartments in ix and x; absence of a primary loop on the anterior region of the male paired duct; simple linear sperm duct in the paramedian chamber lateral to the median regions; absence of an epididymis; presence of a hirudiniform axial acaecate vagina on the recurrent limb of the female median region; and the 3-annulate complete somite which is unique among jawed leeches.

It was noteworthy that some specimens clearly showed the unusual feature of the nephropores in ix and x advanced anteriorly in a₁, not close to the posterior border of the annulus (Fig. 1, B), and in ix placed actually close to the furrow viii/ix.

With the exception of the ocular arch, it can be recognized that the few "haemadipsine-like" features in *Mesobdella* are secondary adaptations to the terrestrial jawed sanguivorous habit. In contrast, the evidence against haemadipsine relationship is found in systems which have not come under the influence of this habit, the female median region and the simple form and paramedian position of the anterior region of the male paired duct, unlike the auriculate land-leeches where the organs on the anterior region of the male paired duct elaborate on a primary loop in the median chamber of the secondary body cavity, a morphological specialization closely related to the terrestrial locomotion and behaviour in these leeches (Richardson, 1969a).

The possession of a "haemadipsine" ocular arch was the primary factor leading Blanchard to a haemadipsine affinity for *Mesobdella*, suitable otherwise since this was a terrestrial jawed sanguivore. The eyes are modified somital sense organs, the 1st pair paramedians, the others intermediates; as such the form of the arch is an expression of the annulation of somites i to vi, somites dedicated to the formation of the anterior sucker as an organ of locomotion and an essential organ of ingestion, with in the leech the process of cephalization secondary to cotylation, the process of sucker formation in which the anterior somites undergo gross levels of morphological reduction. The annulation of the ocular arch becomes secondary to the morphology of the sucking organ and to any specialized functional requirements placed on this organ.

In sanguivores and macrophages of the aquatic and amphibious habit, iii and iv are incomplete; iii uniannulate, the last somite of the velum proper; iv, 2-annulate forming a dorsolateral lobe on the margin of the sucker. In terrestrial jawed sanguivores, iii is uniannulate; iv either uniannulate, or 2-annulate across the median and paramedian fields, and uniannulate laterally; no dorsolateral lobe is formed on the margin of the sucker. The annulation of these somites is of this pattern in 4-, 5- and 6-annulate haemadipsines, is independent of the general level of somital annulation, and to be recognized as a morphological adaptation to the terrestrial sanguivorous habit.

The "haemadipsine" ocular arch in *Mesobdella* shows that the leech is sanguivorous and terrestrial in habit, and is not evidence that the leech is haemadipsine. The presence of such an arch is not evidence of a haemadipsine relationship for the g. *Diestecostoma* of Mexico and Guatemala, similar to *Mesobdella* (Caballero, 1940; Ringuelet, 1944a; Moore, 1946) in the ocular arch (but with 2 annuli between 4 and 5); in the small posterior sucker (but without radial muscles and clamp); obscure small somital sense organs; ventral nephropores with the 17th pair of nephridia opening by a common median ventral pore; lacking auricles; with tall distinct jaws; differing in being 10-annulate on complete somites, with bimyomeric megamorphic regions and consequent from this the epididymis shifted posteriorly on a secondary loop and the ovaries secondarily posterior to the median region (as in the megamorphic condition in the Oriental hirudiniform *Whitmania acranulata* and *W. gracilis*; Richardson, 1969b).

The differences between *Diestecostoma* and typical haemadipsine morphology as known to him, led Moore (1946) to propose a relationship to the Palaearctic g. *Xerobdella*, this having an "haemadipsine" ocular arch, the nephropores as in *Diestecostoma*, trignathous, tall jaws, 5-annulate complete

somites, etc. For these two genera, Moore proposed a s.f. Xerobdellinae to stand with the Haemadipsinae and Hirudininae in the Hirudidae, and later set apart as the F. Diestecostomatidae Ringuélet (Soos, 1966). This was the first time that the "haemadipsine" ocular arch was recognized as other than exclusively haemadipsine. Although a possible relationship of *Mesobdella* and *Diestecostoma* had been anticipated (Ringuélet, 1944), and considered by Moore (1946), *Mesobdella* remained in the Haemadipsidae.

As has been demonstrated with the hirudiniform leeches (Richardson, 1969b), a megamorphic condition of bimyomeric median regions on the reproductive systems is only of generic value. *Diestecostoma*, *Mesobdella*, and *Nesophilaemon* possess in common with the Neotropical aquatic sanguivores: the paramedian position of the organs on the anterior region of the male paired ducts, the absence of a primary loop on this duct, the lack of ejaculatory bulbs, and an acaecate vagina; a morphology separating *Nesophilaemon* and *Mesobdella* from the Haemadipsidae and indicating that the relationship of all three genera will be found among the leeches of the Neotropical Region.

Although previously I had recognized the morphology of the reproductive systems in the Neotropical g. *Oxyptychus* as characterized by the acaecate vagina, I then saw this only as associating the genus with the aquatic jawed sanguivores in the Mexican genera *Limnobdella* (= *Potamobdella*) and *Pintobdella*, and the North American g. *Macrobdella*. This is supported by a conformity in the nature of the pharynx and related structures. I realize that my action in centering this group on the g. *Macrobdella* has zoological foundation in comparative morphology but requires reassessment.

I am now aware that in the case of the Neotropical agnathous macrophagous g. *Semiscolea* I allowed myself to suggest haemopisoid affinities because I attached undue importance to the haemopisoid nature of the pharynx and related structures contrary to the clear indications from the absence of an ejaculatory bulb and the possession of an acaecate vagina, both without parallel in the Haemopidae.

It is recognizable now that the leeches in the g. *Semiscolea* are Neotropical. They have a mesomorphic female reproductive system with an acaecate vagina; lack ejaculatory bulbs; and although there appears to be a loop on the anterior region of the male paired duct, this is not primary but secondary, a development related to the megamorphic condition of the male median region as can be seen from the differing relationships of the epididymis in the species described by Ringuélet (1944b) in contrast to the stability in relationship shown in the members of the Haemopidae.

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